Early Journal Content on JSTOR, Free to Anyone in the World

This article is one of nearly 500,000 scholarly works digitized and made freely available to everyone in the world by JSTOR.

Known as the Early Journal Content, this set of works include research articles, news, letters, and other writings published in more than 200 of the oldest leading academic journals. The works date from the mid-seventeenth to the early twentieth centuries.

We encourage people to read and share the Early Journal Content openly and to tell others that this resource exists. People may post this content online or redistribute in any way for non-commercial purposes.

Read more about Early Journal Content at http://about.jstor.org/participate-jstor/individuals/early-journal-content.

JSTOR is a digital library of academic journals, books, and primary source objects. JSTOR helps people discover, use, and build upon a wide range of content through a powerful research and teaching platform, and preserves this content for future generations. JSTOR is part of ITHAKA, a not-for-profit organization that also includes Ithaka S+R and Portico. For more information about JSTOR, please contact support@jstor.org.

A STUDY OF THE VEGETATION OF THE MESA REGION EAST OF PIKE'S PEAK: THE BOUTELOUA FORMATION.

II. DEVELOPMENT OF THE FORMATION.

H. L. SHANTZ.

(WITH SIX FIGURES)

In an earlier paper[1] the writer has discussed the structure of the Bouteloua formation, and to this publication the reader is referred for general introductory matter. Space will not permit the inclusion here of lists of species in the formations of minor importance, which have to do with the development of this formation. The foothill thicket formation, the plains ruderal formation, and the plains bank formation are each made up of many species. Only the facies and a few of the more important principal species can be mentioned.

Invasion by formations.

FOOTHILL THICKET FORMATION.

This formation extends along the eastern base of the mountains and down along the ridges and gullies far out on the plains. It forms a distinct zone at the base of the mountains (*fig. 8*) and here occurs in its best developed form. In most places under natural conditions there seems to be an ecotone, a place of equal aggressiveness, between this formation and the Bouteloua formation.

FACIES: Cercocarpus parvifolius H. & A., Rhus trilobata Nutt., Quercus novo-mexicana (DC.) Rydb., Q. utahensis (DC.) Rydb., Q. Gambellii Nutt.

PRINCIPAL SPECIES: Rubus deliciosus James, Holodiscus dumosus (Nutt.) Heller, Ribes cereum Dougl., R. leptanthum Gray, R. pumilum Nutt.

In addition to those named there are about one hundred principal and secondary species.

This formation and the Bouteloua formation seldom mix, because where the shrubs grow the facies of the grass formation cannot exist. Nearer the mountains and along the hillsides they alternate sharply.

While the climatic and soil conditions are identical, the difference in cover causes great difference in physical factors. Simultaneous physical factor readings show very clearly these differences. The following is a typical set:

---

[1] BOT. GAZETTE 42:16–47. 1906.

Aug. 3, 1904, 10:45 a. m.

	LIGHT	TEMPERATURE					REL. HUMIDITY		WATER CONTENT
		Soil	Soil surface	Plant surface	10^{cm}	1^{m}	10^{cm}	1^{m}	
Open............	6s	24°	50°	44°	29°6	28°4	40%	32%	3.6%
Thicket (Quercus)	180s	18°	30°	28°2	27°2	26°8	42%	39%	8.3%

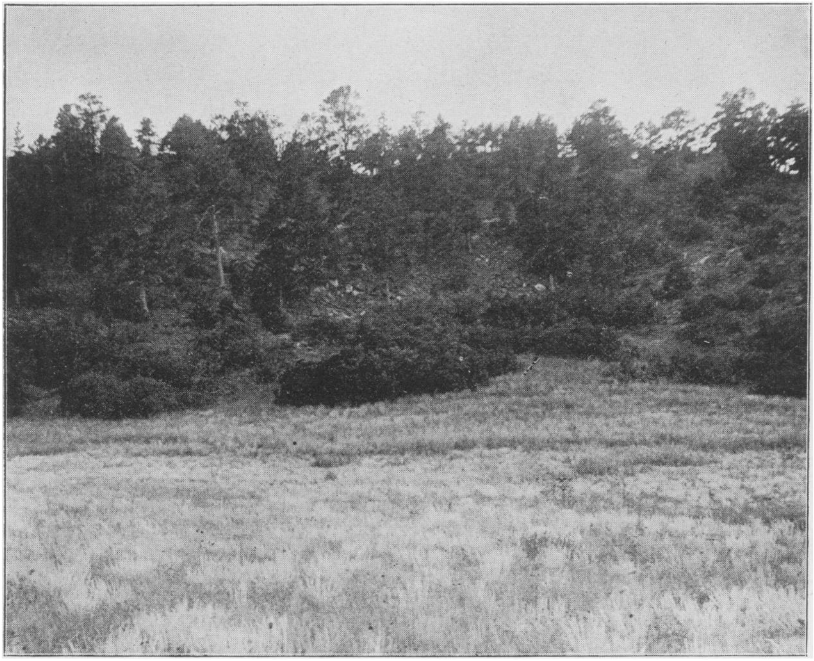

FIG. 8.—Zonation at Palmer Park; frontal zone of *Bouteloua oligostachya* and *Artemisia frigida;* zone near base of the bluff *Andropogon furcatus;* at the base of the bluff the foothill thicket (Quercus); the bluff showing pine formation (*P. scopulorum*).

These conditions existed on the same exposures and 6^{m} apart. The open quadrat was dominated by *Bouteloua oligostachya* and *Artemisia frigida;* while the shaded quadrat contained *Quercus utahensis,* *Coleosanthus umbellatus*, *Oryzopsis micrantha*, *Elymus condensatus*, *Filix fragilis*, and *Bryum argenteum*. The thicket was rather open, as may be seen at once by the light readings, the ratio of which is $\frac{1}{30}$. This ratio often becomes $\frac{1}{60}$, but is usually less for the greater part of the formation.

Along the ridges north and east of Colorado Springs there is certain evidence that the thicket formation is slowly pushing its way out into the grass formation. Of the shrubs *Cercocarpus parvifolius* seems best adapted for this invasion, and it is several miles in advance of any of the other dominant species (*fig. 9*). Nearer the mountains evidence is also found of the invasion of the grass formation by the thicket formation. This invasion, however, is not rapid. As soon as the young shrub is established or has grown to sufficient size to produce shade, the grass formation gives way rapidly to species

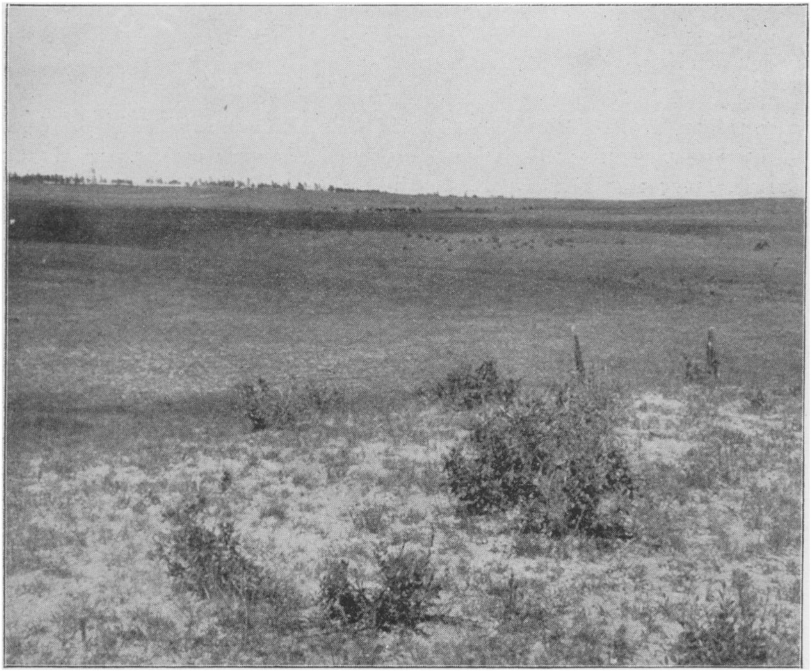

FIG. 9.—*Cercocarpus parvifolius* invading the Bouteloua formation; pine formation on the horizon.

of the thicket formation. Among the first species to appear in the shade of these advancing shrubs are *Calochortus Gunnisonii*, *Mertensia linearis*, and *Stipa neo-mexicana*. Later, when the habitat has been rendered less xerophytic and when the other facies have entered, *Coleosanthus umbellatus*, *Oryzopsis micrantha*, *Elymus condensatus*, *Selaginella rupestris Fendleri*, *Filix fragilis*, and a number of other species appear.

Under perfectly natural conditions and without the intervention of herbivora, the thicket would undoubtedly replace the greater part of the grass near the mountains, but, as is seen later, the thicket is slowly giving way and the grass formation is advancing.

PLAINS RUDERAL FORMATION.

FACIES: Stipa Vaseyi Scribn., Puccinia Stipae Arth., Boebera papposa (Vent.) Rydb., Helianthus petiolaris Nutt., Puccinia Helianthi Schw., Thelesperma intermedium Rydb., Verbena bracteosa Michx., Amaranthus blitoides S. Wats.

PRINCIPAL SPECIES: Salvia lanceolata Willd., Lappula occidentalis (Wats.) Greene, Polygonum aviculare L., Erysiphe Polygoni DC., Munroa squarrosa (Nutt.) Torr., Salsola Tragus L., Euphorbia glyptosperma Engelm., Malvastrum coccineum (Pursh) Gray, Puccinia Malvastri Pk., Vicia americana, Aecidium porosum Pk., Solanum rostratum Dunal, Helianthus annuus L., Cleome serrulata Pursh, Schedonnardus paniculatus (Nutt.) Trelease, Atriplex argentea Nutt., Senecio spartioides Torr. & Gray, Verbesina encelioides (Cav.) Gray, Helianthus petiolaris Nutt., Puccinia Helianthi Schw., Picradeniopsis oppositifolia (Nutt.) Rydb.

The secondary species of this formation are very numerous.

The physical factors of this formation are practically the same as those given for the Bouteloua formation. The conditions of water content are such that the most common ruderals, eastern and European species, cannot thrive to the best advantage. Many native plants behave as ruderals and this name is applied to the formation. This formation represents many different stages in a succession which will result ultimately in the grass formation, and is always invaded by the plants of the grass formation. Only a few of the ruderal species succeed in the grass formation. The most important of these is *Boebera papposa*, occurring everywhere throughout the formation and sometimes very abundant. It is much better developed in a ruderal position and is regarded as a part of the ruderal formation. *Stipa Vaseyi*, another native plant, succeeds best in ruderal positions, but is often found as part of the formation.

The species of the ruderal formation are almost entirely native plants which readily invade any area from which the vegetative covering has been removed. Of the true ruderals, *Salsola Tragus* pushes its way into the formation proper. Here it occurs as dwarfed plants which seldom branch, and which die during the aestival period. *Leptilon canadense*, which occurs only here and there in the ruderal formation, also occurs throughout the grass formation. The plants are usually reduced to 10^{cm} in height.

PLAINS BANK FORMATION.

Whenever a ditch is made through the grass or other formations, or where the grass formation is irrigated, the bank formation comes in. It matters not what kind of soil, the presence of an abundance of water enables this formation to succeed. This, however, is not true invasion, and comes about only as a result of changed conditions which make the existence of the grass formation impossible. Good examples of the coming in of the bank formation may be found in irrigated meadows and in small areas where irrigation ditches or reservoirs have leaked.

A study of this formation is of the greatest interest, for it is along this formation that the eastern species find their way into the region. The reason is obvious, for here they find suitable conditions of water supply. As a result, it is here that the vegetation is made up of the most widely distributed species.

The mountain species find in this formation the cool temperature that enables them to exist away from their natural habitats. These species pass down along the brook banks, while the eastern species pass up along these same banks. The result is a varied flora.

The radical difference in water content between this formation and the Bouteloua formation does not permit of direct invasion. The following species, however, may occur in either formation: *Erigeron flagellaris*, *Agropyron occidentale*, *Helianthus annuus*, *H. petiolaris*.

The facies of the bank formation varies greatly with the age of the formation. In the ultimate stage they are as follows:

Populus deltoides Marsh., P. angustifolia James, P. acuminata Rydb., Salix spp., Prunus melanocarpa (A. Nels.) Rydb., P. americana Marsh., Rosa Sayi

Schwein., Ribes aureum Pursh, Clematis ligusticifolia Nutt., Symphoricarpos occidentalis Hook., Rhus trilobata Nutt.

In an earlier stage this formation is found best developed in the irrigated meadows where *Poa pratensis* L., *Eragrostis alba* L., *Juncus balticus* Willd., *Heleocharis palustris* (L.) R. & S., and *Medicago sativa* L. may rank as facies.

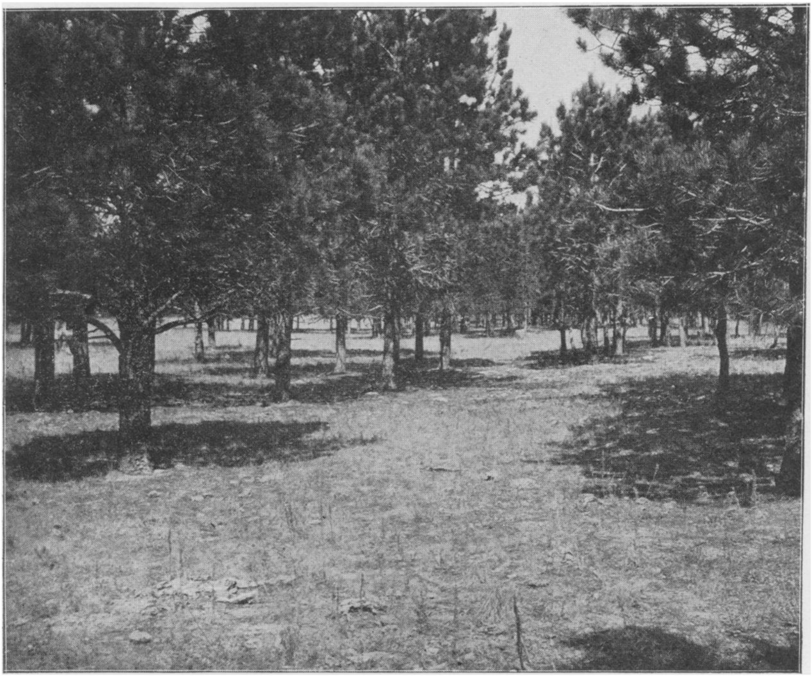

Fig. 10.—Floor of the pine formation (*P. scopulorum*) covered with the Bouteloua formation (*B. oligostachya*, *Koeleria cristata*, and *Artemisia canadensis*).

Xanthium commune and *Melilotus alba* are among the very first plants to enter on a newly formed ditch bank. In this formation are found many of the common species which occur in mesophytic situations in the eastern part of the United States.

PINE FORMATIONS.

As CLEMENTS[2] has pointed out, there are two pine formations near the base of the mountain range, the "foothill woodland" and the "pine." The first has as facies *Pinus edulis* Engelm. and *Juniperus monosperma* (Engelm.) Sarg.; and as principal species, *Stipa Scribneri* Vasey. The second has as facies *Pinus scopulorum* (Engelm.) Lem. and *P. flexilis* James.; and as principal species, *Arctostaphylos Uva-ursi* (L.) Spreng.

---

[2] Univ. Neb. Studies 4: no. 4. 1904.

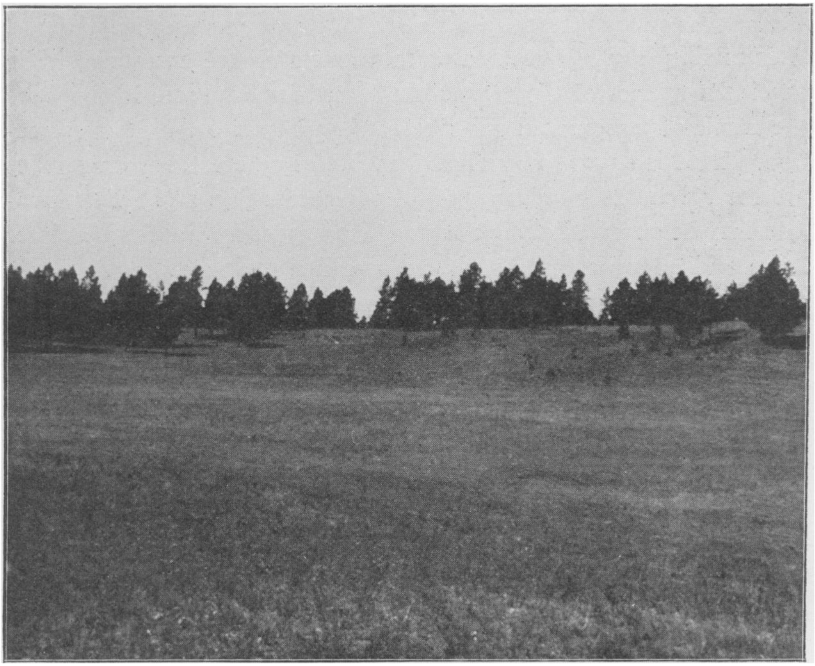

FIG. 11.—*Pinus scopulorum* invading the Bouteloua formation.

In the zone at the base of the mountains lies the foothill woodland formation, while just above is the pine formation. Each of these formations is invading the Bouteloua formation, and the one which lies higher on the mountains, the pine formation, is the more successful.

A consocies of this formation dominated by *Pinus scopulorum* has pushed its way eastward far into Nebraska[3] and carries with it many of the principal and secondary species. *P. flexilis* drops out before the foothills are reached. Near Eastonville, Colo., this formation may be seen meeting the Bouteloua formation. All along this ridge the thicket formation has dropped out and the pines advance alone. The forest is not dense, and while many of the principal and secondary species are found on its floor, plants are also found which belong to the grass formation and which are able to survive in this location. In fact, the grass formation is found here in places dominating the floor of the pine formation—a true mixing of the formations (*fig. 10*). This mixing may be due to a certain extent to the entrance of the dominant species of the grass formation, but it is more likely to be the result of the gradual advance of the pines into the grass formation. This is shown very clearly in places where the young pines are several meters in advance of the older trees (*fig. 11*). This invasion may be observed along the ridge leading eastward from Palmer Lake and on which is found the so-called "black forest." Here the pines and the grasses mix and there are no shrubs present (*fig. 10*). The principal species, *Arctostaphylos Uva-ursi*, is also pushing out into the grass formation. A short distance west of Pring, Colo., this pine formation may be seen rapidly advancing along an old roadbed.

---

[3] POUND and CLEMENTS, Phytogeography of Nebraska, 2d ed., Lincoln, Neb., 1900, p. 336.

An entirely different condition may be observed eleven miles east of Colorado Springs. Here the pine formation is also advancing, but it is accompanied or rather preceded by the thicket formation. The advance of these two formations is favored by the cutting back of the gullies, forming steep hillsides, which offer the most favorable conditions for the growth of these two invading formations.

In many places the thicket, pine, and grass formations are found to meet and mix equally, the grasses forming the floor between the shrubs, and the pine scattered throughout. These three important formations are not only found meeting here on equal terms, but a remnant of an older formation, or at least one which gives evidence of greater age, is also found. This is the foothill woodland. *Juniperus monosperma* is scattered here and there and isolated trees of this species are often found which seem to be very old. Still stronger evidence is found in the fact that here, many miles removed from its fellows, is a very large and apparently very old *Pinus edulis*. Erosion has removed the soil from the base of the tree, exposing the roots, and it is certainly much older than any of the other trees in this region. It is the only tree which supports a rich lichen flora.

Four important formations are found meeting and mixing here: the oldest, the foothill woodland, which has almost disappeared; the pine formation, which is slowly advancing; the thicket formation, which is also gradually advancing; and the grass formation, which gives way as the others advance. The thicket formation at this point entirely lacks the oaks, which fact is probably due to grazing.

In another part of the grass formation there is evidence of a slight advance of the foothill woodland. Young trees of *Juniperus monosperma* have established themselves in a few places on the mesa. In other places *Stipa Scribneri* is entering the plains region along with the thicket formation. The preponderance of evidence, however, seems to be in favor of a recession of this formation, and there is good reason to believe that it was at one time more extensive than at present.

Many species which seem to be most at home in the mountain formations also push down into the Bouteloua formation. Among these may be noted *Achillea lanosa*, extending down the draws, *Geranium caespitosum*, *Gilia pinnatifida*, *G. aggregata*, *Campanula petiolata*, and many other species.

Succession.

PRIMARY SUCCESSION.

On rock.

What the primary succession has been in this region cannot be determined. The succession on rock undoubtedly began with the lichen. On the most exposed rocks of the lime ridge *Staurothele umbrina* and *Lecanora previgna* are practically the only lichens found. On the other rocks the lichens are much more mixed and there seems to be good evidence of the accepted succession for lichens: first the crustose; then the more foliose forms like *Lecanora rubina* and *L. rubina opaca;* and finally *Parmelia conspersa.* On the mesa, where the rocks range from 5^{dm} in diameter to coarse gravel, *Parmelia conspersa* is the most important lichen, although *Rinodina oreina* and *Lecanora calcarea* are also common. *Placo-*

dium elegans, which is also common on rock, seems to require protection and is probably one of the later species to appear. The same may be said of *Lecanora subfusca allophana*, one of the important lichens, which succeeds best in crevices.

The rock lichens occurring within this region belong to the primitive lichen formation.

FACIES: Parmelia conspersa (Ehrh.) Ach., Rinodina oreina (Ach.) Mass.

PRINCIPAL SPECIES: Lecanora calcarea (L.)Sommerf., L. subfusca allophana Ach., L. previgna (Ach.) Nyl., L. rubina (Vill.) Ach., L. rubina opaca Ach., Placodium elegans (Link) DC., Buellia petraea montagnaei Tuck., Lecanora previgna revertens Tuck., L. xanthophana dealbata Tuck., Staurothele umbrina (Wahl.) Tuck.

SECONDARY SPECIES: Placodium cerinum (Hedw.) Naeg. & Hepp., Acerospora chlorophana (Wahl.) Ach., Biatora crenata dealbata Tuck., Heppia Despreauxii (Mont.) Tuck., Placodium vitellinum (Ehrb.) Naeg. & Hepp., Umbilicaria rugifera.

This formation occurs on all exposed rocks, with the possible exception of the Permian, which in most places disintegrates too rapidly to support a lichen flora. With the exception of the last four species, all of the species occur on exposed surfaces. The last four and *Placodium elegans* prefer shaded or at least somewhat protected situations. Throughout the mesa this formation has been almost completely replaced by the Bouteloua formation. On hills and more exposed rocky situations it is sometimes as important as the grass formation with which it alternates. With the more complete disintegration of the rocks this formation will entirely disappear.

On alluvium.

Uncertain as is our knowledge of the primary succession on rock, it is much more certain than our knowledge of the primary succession on alluvium. A careful study of the formation, and in particular those places which are least covered with vegetation, seems to aid in forming an idea of this primary succession.

Near Eastonville, in the region lying between the Bouteloua formation and the invading pine formation, an open area is being invaded by the following species: *Potentilla coloradensis*, *Thermopsis rhombifolia*, *Erigeron glandulosa*, *Paronychia Jamesii;* followed by *Arenaria Fendleri*, *Muhlenbergia gracilis*, *Bouteloua oliogostachya*, *Gutierrezia Sarothrae*, *Artemisia canadensis*, and *Tetraneuris glabriuscula*. This is probably the best example of primary succession found by the writer. The absence of ruderal species is especially noticeable.

On the mesa the *Andropogon scoparius* consocies seems to be most primitive. In places not yet covered with vegetation, where the alluvium is nearest what it seems to have been originally, this grass is most abundant and together with *Eriocoma cuspidata* is the first to disappear in passing from this exceedingly open association to the more stable or closed Bouteloua formation. *Eriognum alatum*, *E. Jamesii*, *Tetraneuris glabriuscula*, and *Machaeranthera cichoracea* are generally present; but since they extend into the true Bouteloua formation they are probably not as much a part of the primitive association as the plants mentioned above.

The lime ridge vegetation is probably primitive, as shown by the following quadrat:

Lesquerella alpina	52	Oreocarya thyrsiflora	3
Gutierrezia Sarothrae	5	Gaura coccinea	1
Lithospermum linearis	4	Machaeranthera cichoracea	1

Total surface covered, 5 to 6 %.

At some distance from this, a quadrat shows the following:

Lesquerella alpina	31	Eriogonum Jamesii	3
Grindelia squarrosa	14	Boebera papposa	3
Hedeoma nana	13	Lithospermum linearis	1
Gaura coccinea	8	Salsola Tragus	2
Bouteloua oligostachya	6	Eurotia lanata	1
Aristida longiseta	4	Machaeranthera cichoracea	1
Stipa Vaseyi	3		

Total surface covered, 7 to 8%.

The entrance of Bouteloua is already noted, as is *Aristida longiseta*. A more distant point will show the following quadrat:

Bouteloua oligostachya	54	Lithospermum linearis	6
Atheropogon curtipendulus	28	Aristida longiseta	3
Grindelia squarrosa	16	Eriogonum Jamesii	2
Boebera papposa	57	Pentstemon angustifolius	1
Malvastrum coccineum	7	Salvia linearis	2
Lesquerella alpina	6	Stipa Vaseyi	1
Helianthus annuus	8	Salsola Tragus	2
Gutierrezia Sarothrae	13	Artemisia frigida	3
Chenopodium leptophyllum	10	Evolvulus pilosa	1

Total surface covered, 18 to 20%.

These quadrats are all on steep slopes where the soil is more or less broken. The first quadrat is in pure disintegrated limestone; some gravel has been washed into the second quadrat; while the third is a mixture of gravel, clay, and lime. The difference in soil is of no importance in this connection, since in other places the same succession occurs on the pure disintegrated limestone. In the first quadrat the water content varies from 19 to 6%; in quadrat 3 it varies from 19 to 2%; while in the second quadrat the per cent. of water is intermediate. As one passes from the first quadrat to the second and then to the third, the facies of the Bouteloua formation are found making their appearance; in fact, the flora, aside from a few ruderal species and *Lesquerella alpina*, is decidedly of the Bouteloua formation.

The native species, which are referred to as ruderal, show the greatest ability to occupy new ground and they are the most important in secondary succession. It seems reasonable to suppose that they were also very active in invading the newly formed alluvium, and that, if any of the existing species have taken part in the primary succession, these plants are to be sought among the native ruderals. This can be more clearly understood after a consideration of secondary succession.

SECONDARY SUCCESSION.

The repeated changes which have taken place in the formation of the great plains have manifestly been accompanied by changes in vegetation. What these changes have been can only be inferred from the changes which are now taking place wherever, in the process of erosion, there is a cutting away or deposition of material. These successions in a certain sense are primary, but will be discussed under secondary successions.

Biotic agencies.

There are so many chances for observing secondary successions that the experimental denuded quadrat was not deemed necessary, although several of these are now under observation. There are many trails which lead through the Bouteloua formation where the ground has been but slightly disturbed (*fig. 12*). The travel has simply worn off and killed the original vegetation. After having been in use for a longer or shorter time they are generally abandoned. The soil is hard, in fact has never been broken, but since there is no vegetation, an opportunity is afforded for the entrance of new plants. These trails have not been used in wet weather, and they are therefore never cut up and no loose soil is formed. The succession here is first ruderals like *Boebera papposa*, *Amaranthus blitoides*, or *Verbena bracteosa*. These seem to be most successful invaders of such trails. The grasses of the formation come in slowly, *Muhlenbergia gracillima* generally in advance of, or with *Schedonnardus paniculatus*, *Sitanion elymoides*, *Athero pogon curtipendulus*, and ultimately *Bouteloua oligostachya*. It is not an uncommon thing to find these old trails only distinguishable by the depression of surface and completely covered by the *Muhlenbergia gracillima* consocies. Where the same trail leads through the purer growth of *Bouteloua oligostachya*, it is not so rapidly covered, and when it passes through the *Bouteloua hirsuta* consocies it remains open for a still longer period.

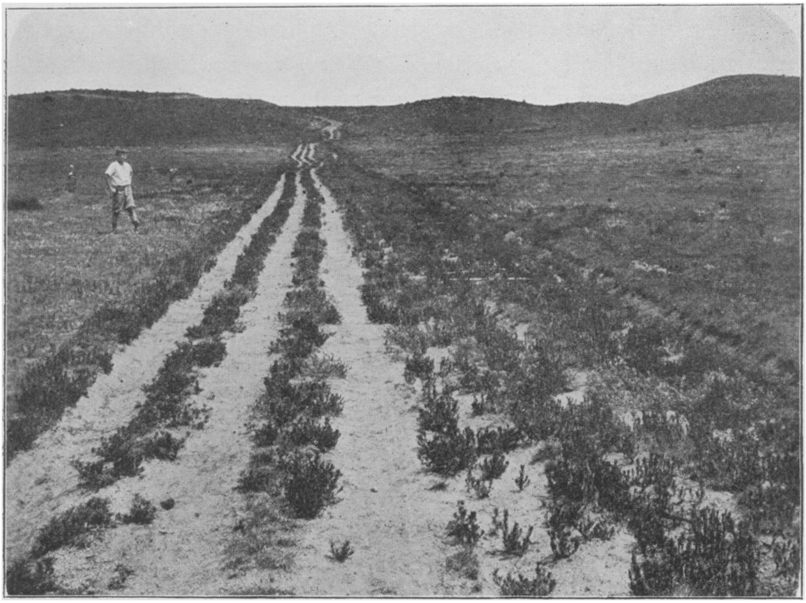

FIG. 12.—Trail invaded by *Boebera papposa;* Bouteloua formation at the sides.

The mesa road was originally of the type just mentioned. During wet weather the road would be cut up to a certain extent and drivers would then turn to one side in order to escape the rough road. The new path has always been formed on the southwest side. This road has been in constant use for several years with the result that plants have been destroyed continually on one side, and have invaded the old roadways from the other. These old roadways show a great many stages in succession.

The road is left in a somewhat roughened condition and the most important species to enter is *Stipa Vaseyi*. It thrives best in newer situations and disappears gradually as one passes back from the well-formed frontal zone. The stable condition which it brings about is not favorable for the growth of the seedlings and it dies out after ten to fifteen years. Aside from the entrance of the annual ruderals *Boebera papposa*, *Amaranthus blitoides*, and *Verbena bracteosa*, it represents the first stage in the succession which will result ultimately in the *Bouteloua oligostachya* formation.

The species which ultimately take possession are usually determined by the adjacent formation. Where *Muhlenbergia gracillima* is dominant it usually appears much in advance of *Bouteloua oligostachya*; but where the latter is dominant, it is usually in advance. *Stipa Vaseyi*, the first perennial to appear, is usually accompanied by the annuals *Boebera papposa*, *Salvia lanceolata*, *Polygonum aviculare*, *Amaranthus blitoides*, and a number of other species. The grasses enter in about the following order: *Schedonnardus paniculatus* followed by *Sitanion elymoides* and *Aristida longiseta*, and ultimately by *Muhlenbergia gracillima* and *Bouteloua oligostachya*. With these grasses there appear many annual ruderals and also the following: *Senecio spartioides*, *Gutierrezia Sarothrae*, *Artemisia frigida*, *Carduus undulatus*, *C. plattensis*, and *Pentstemon angustifolius*.

A transect of the mesa road will give more detailed information regarding the sucessions found here (see transect). This transect is one meter wide. In the plot each division represents one meter, and the most important species in each square meter is placed at the left, and the other species in order of their importance are added to the right.

Bouteloua Formation		Bo	M		B	G					S		
		Bo	M	B		Af		G					
		Bo	B	M		Af		G					
Old roadways — the oldest near the top		Bo	M	Sv	B	Af	Sl	G	Ss				
		SP	M	B	Sv	Bo	Af	G	Cu		Sl	Ss	
		M		Bo	B	Sv	SP	Ad	Af	Va	Cl		
		SP	Sv	Ss	G	B	Sl	Cu	Mc				
		SP	G	Ss	Ad	Af	Mc	Cu	So		Va		
		SP	Sv	Bo	G	B	Sl	Al	Cu				
		Bo				Sv	B	Sl	G	Y	M		
		Bo	Sv	Sl	Ss	Cl			Al				
		Sl	B	Sv	Ss	SP	M			St	So	Str	
		B	SP	Sv	Sl	Vb		Se	Pa	St	S	Ss	Te
		B	SP	Sv	M		Sl	Mc	Cl	G	S	Va	Pa C Sc
		Sv	Se	B	Cl	Sl		Pa			C		
		Sv		Se	B	Sl		Ss	Ad	Af	Va	Cl	
		SP	Sy	B	Sl	So	Ad	G	Cl	Ss	Va	S	
		Sv	B	Bo	SP	Se	Cl		Sl				
		B	Sp	Sv	Cl	Va	Sl	L	Pa	Te			
		B	SP	Sv	Cl	Va	Ad						
		B	Sv	Cl	Sp		Sl	Ss					
		B	Sv	Aa			Sp	Sl	Y	Pa	S	Se	
		Sv	B	Sl							Va		
		Sv	B	Sl			St	Sc	Ab	Ca	I	Pa	
ROAD													
									B				
							B		Aa				
				B	Aa			Ss					
				B			S	Ss	Aa				
		B	Bo				Mc						
Bouteloua formation		Bo		B			S	G	Ss				
		Bo		B			Y	Ss	Tg	Te			
		Bo	B			Y	Sp		G	S			
		Bo	Tg	B	Al	M	Ad	G	S	Ee			
		Bo	A	M	L	B	S	Ad	Tg	Te	Ee		
		Bo		M	G	Bh	A	B	Ss	S			

A,	Atheropogon curtipendulus
Aa,	Atriplex argentea
Ab,	Amaranthus blitoides
Ad,	Astragalus Drummondii
Af,	Artemisia frigida
Al,	Aristida longiseta
B,	Boebera papposa
Bh,	Bouteloua hirsuta
Bo,	Bouteloua oligostachya
C,	Calamovilfa longifolia
Ca,	Cycloloma atriplicifolium
Cl,	Chenopodium lepidophyllum
Cu,	Carduus undulatus
Ee,	Eriogonum effusum
G,	Gutierrezia Sarothrae
I,	Iva xanthifolia
L,	Lappula occidentalis
Mc,	Malvastrum coccineum
Pa,	Polygonum aviculare
S,	Sideranthus spinulosus
Sc,	Sporobolus cryptandrus
Se,	Sitanion elymoides
Sl,	Salvia linearis
So,	Senecio oblanceolatus
Sp,	Schedonnardus paniculatus
Ss,	Senecio spartioides
St,	Salsola Tragus
Str,	Solanum triflorum
Sv,	Stipa Vaseyi
Te,	Townsendia exscapa
Tg,	Tetraneuris glabriuscula
Va,	Vicia americana
Vb,	Verbena bracteosa
Y,	Yucca glauca

TRANSECT OF MESA ROAD.

This transect is typical of the greater part of the road. Near Gleneyrie *Machaeranthera cichoracea* appears in abundance in the frontal zone. At the lower end of the mesa road is found considerable variation. *Cleome serrulata* forms the frontal zone, and with this *Boebera papposa*, *Xanthium commune*, *Polygonum aviculare*, *Verbena bracteosa*, *Munroa squarrosa*, *Amaranthus blitoides*, *Solanum rostratum*, *Chenopodium album*, and *Malvastrum coccineum*. Just back of this, on a portion of the old roadway, is *Stipa Vaseyi*, with *Boebera papposa*, *Euphorbia dentata*, *Chenopodium leptophyllum*, *Ambrosia artemisifolia*, *Sophora sericea*, *Polygonum aviculare*, *Schedonnardus paniculatus*, *Bouteloua oligostachya*, *Muhlenbergia gracillima*, *Artemisia frigida*, *Xanthium commune*, *Carduus undulatus*, *Iva xanthifolia*, *Asclepias pumila*, and *Salvia lanceolata*. The advance on the graded graveled part is made almost entirely by annuals, *Boebera papposa*, *Verbena bracteosa*, *Amaranthus blitoides*, or in rare cases *Solanum rostratum* is most important, while other species are generally present in reduced numbers. The soil in these cases has been packed down and *Stipa Vaseyi* does not enter.

The old mesa road is not followed by the new in all places. In the lower end of the mesa it turns to one side. Here through the original formation, it was only a path. It had been worn down and when abandoned the soil, through the agency of frost and rain, had loosened and fallen in at the sides. This road is now revegetated with *Stipa Vaseyi*, which is in many places replaced by *Muhlenbergia gracillima* and *Bouteloua oligostachya*. In one place this vegetation is practically identical with the formation.

The successions on trails vary considerably in different parts of the region. As one travels from Colorado Springs to Palmer Lake changes are soon noted. A short distance above Colorado Springs *Boebera papposa* becomes less abundant and the first species to invade the roadway is *Plantago Purshii*. Above Monument *Stipa Vaseyi* drops out as an invader, and the principal species which enter are *Polygonum aviculare*, *Lappula occidentalis*, *Verbena bracteosa*, *Amaranthus blitoides*, *A. retroflexus*, *Salvia lanceolata*, and *Rumex acetosella*. Below Monument a short distance the following succession was noted: The advancing zone was made up of *Lepidium* *apetalum*, *Polygonum aviculare*, *Artemisia frigida*, *A. canadensis*, *Verbena bracteosa*, and *Plantago Purshii;* while farther back were found *Bouteloua oligostachya*, *Schedonnardus paniculatus*, *Chrysopsis villosa*, *Arenaria Fendleri*, *Gilia aggregata*, *G. pinnatifida*, *Senecio oblanceolatus*, *Gutierrezia Sarothrae*, *Koeleria cristata*, and *Sitanion elymoides;* followed by the Bouteloua formation in which *Bouteloua oligostachya*, *Stipa comata*, and *Arenaria Fendleri* were most important.

The stages of a succession which converts a denuded trail into the Bouteloua formation are not marked. First there is, as a rule, the entry of many annual ruderal species (*fig 12*). This in many cases is followed by *Stipa Vaseyi*, followed by *Schedonnardus paniculatus*, *Sitanion elymoides*, and *Aristida longiseta*, as well as many other secondary species of the formation, and these in turn by the facies of the grass formation. In some places *Stipa Vaseyi* does not enter and here may be found many other species. Among the more important are *Schedonnardus paniculatus*, *Gutierrezia Sarothrae*, *Chrysopsis villosa*, *Artemisia frigida*, *A. canadensis*, and many other species, followed by the facies of the grass formation.

Near Cheyenne Mountain a number of abandoned corrals show the following as the most important invading species: *Schedonnardus paniculatus*, *Artemisia canadensis*, *Solidago* sp., *Artemisia frigida*, *A. gnaphalodes*, and a number of secondary species—*Petalostemon purpureus*, *Thelesperma gracile*, *Chrysopsis villosa*, *Pulsatilla hirsutissima*, *Lacinaria punctata*, *Sporobolus cryptandrus*, *Aristida longiseta*, *Bouteloua hirsuta*, *Aragallus Lambertii*, and the ruderals *Boebera papposa* and *Euphorbia glyptosperma.*

A denuded quadrat showed during the third summer *Artemisia canadensis*, *Geranium caespitosum*, *Pulsatilla hirsutissima*, *Chrysopsis villosa*, and *Artemisia ludoviciana.* A second corral showed *Artemisia canadensis* and *A. frigida* as the chief invaders, with many other species coming in, of which those most important are *Schedonnardus paniculatus*, *Bouteloua oligostachya*, and *Koeleria cristata.*

The early stages of these successions vary greatly. In the study of a large number the following plants are found to enter first: *Boebera papposa*, in the mesa region and adjacent areas; northward toward Palmer Lake, *Plantago Purshii* or *Polygonum aviculare;*

and farther east *Picradeniospsis oppositifolia*, sometimes accompanied by *Malvastrum coccineum.*

A number of graded roads have been built very recently and these show only the very first vegetation, a ruderal annual vegetation. The boulevard, which runs from Colorado Springs to Manitou, is an older road of this type, having been built for about thirteen or fourteen years. The first permanent succession on this road within the Bouteloua formation was *Stipa Vaseyi*, which is now giving way to *Muhlenbergia gracillima* and *Bouteloua oligostachya.* Many other species came in, among which the more important are *Sitanion elymoides*, *Aristida longiseta*, *Schedonnardus paniculatus*, *Helianthus annuus*, *Quincula lobata*, *Astragalus bisulcatus*, *Sophora sericea*, *Grindelia squarrosa*, with other plants from the formation, as well as ruderal species.

One of the transects of this road deserves special mention. There is a cut here of about 2^m, and the road runs north and south. The differences in the east and west sides are due entirely to the differences in exposure, and to its effect upon temperature and water content. The west side, which receives the most light, has first a distinct zone of *Petalostemon oligophyllus*, back of which there is a mixed zone of *Boebera papposa* and *Xanthium commune;* this is followed on the bank by *Stipa Vaseyi*, and this in turn by a crest zone largely of annuals. The east side shows first a zone of *Xanthium commune* followed by *Stipa Vaseyi*, mixed with *Schedonnardus paniculatus*, *Boebera papposa*, *Psoralea tenuiflora*, etc.; and this is followed on the steep unstable soil by annuals. Back of the annuals is the Bouteloua formation in which *Muhlenbergia gracillima* predominates.

There is a great deal of variation in the species which first appear. Almost any one of the species cited under the ruderal formation may dominate in certain places, but the more or less typical examples mentioned above should serve to give an idea of the succession on roads.

Reservoirs are generally built where only one side needs to be dammed. The outer slope of the dam is invaded in the same way a road would be. An interesting exception is found at Palmer's reservoirs. The large reservoir, which was built in 1902, had by

1904 covered the bank chiefly with *Stanleya glauca* and *Mentzelia decapetala.* A great deal of the soil of this bank was hauled in from the lime ridge region, and with it, the seeds of *Stanleya glauca* were carried in. In one of the other reservoirs, which is several years older, *Medicago sativa* was predominant. Normally, *Boebera papposa, Stipa Vaseyi,* and other ruderals would be expected to appear first.

A new reservoir constructed on the mesa in 1904 showed during 1905 the following species: *Boebera papposa, Salsola Tragus, Senecio spartioides, Artemisia frigida, Senecio oblanceolatus, Argemone intermedia, Mentzelia nuda, Polygonum aviculare, P. Douglasii, Euphorbia robusta, Yucca glauca, Chenopodium album, Gaura coccinea, Cleome serrulata, Petalostemon purpureus, Amaranthus blitiodes,* and *A. retroflexus.*

In building roads and reservoirs it often happens that several meters of surface soil and all the vegetation is removed. Succession is different here from the places already mentioned. The annual ruderals do not appear in such great numbers. Among the species which enter are *Argemone intermedia, Mentzelia ornata, Petalostemon oligophyllus, P. purpureus, Sitanion elymoides, Aristida longiseta, Munroa squarrosa,* and other common hillside plants, since the soil here is usually gravel.

Broken areas.

Here and there on the plains are found areas which have been plowed and planted, but have been abandoned because of the scanty water supply. The succession of plants here is much the same as on graded roads, but is usually more uniform. An abandoned garden patch showed the following year the facies *Anogra albicaulis,* with *Chenopodium album* and *Helianthus annuus* as the principal species. An area on top of the mesa showed almost a pure stand of *Boebera papposa;* while still another showed *Schedonnardus paniculatus. Artemisia frigida* sometimes enters denuded areas and dominates the early stages of the succession. During 1904 a tract was seeded with *Lolium perenne;* the following summer it showed *Boebera papposa* and *Verbena bracteosa,* as well as *Polygonum aviculare, Salsola Tragus, Artemisia frigida, Lolium perenne,* *Solanum triflorum*, *Senecio oblanceolatus*, and *S. spartioides;* also a very few young plants of *Yucca glauca*, *Argemone intermedia*, *Carduus undulatus*, and *Tetraneuris glabriuscula.*

The usual flora on the hills of the prairie dog is *Anogra coronopifolia*, *Malvastrum coccineum*, *Munroa squarrosa*, *Amaranthus blitoides*, *Picradeniopsis oppositifolia*, *Boeberá papposa*, and *Artemisia frigida*. *Muhlenbergia gracillima* is the most effective in reclaiming the old deserted hills. In fact, in looking over a deserted dog town the location of the old dog hills can be determined at once from the fact that although the surrounding vegetation is dominated by *Bouteloua oligostachya*, the location of the old hills is marked by a community of *Muhlenbergia gracillima.*

Near Pring, Colo., an abandoned field showed the first year *Helianthus petiolaris*, with a less amount of *Boebera papposa*, *Malvastrum coccineum*, *Solanum rostratum*, *Lappula occidentalis*, *Verbena bracteosa*, and a very few plants of *Artemisa frigida*, *Atheropogon curtipendulus*, *Schedonnardus paniculatus*, *Carduus undulatus*, and *Eriogonum annuum*. Here are found three very distinct sets in the succession. First, annual species, followed by a group of ruderal species, and this in turn by perennials from the Bouteloua formation. In another place *Thelesperma intermedium* was the first species to enter. Near Falcon, Col., an abandoned field showed after two years *Helianthus petiolaris* and also *Munroa squarrosa*, *Lappula occidentalis*, *Chaetochloa viridis*, *Plantago Purshii*, *Amaranthus retroflexus*, and *Ptiloria ramosa*. In some places *Bouteloua oligostachya* was entering. Another field which had been abandoned for about eight years showed *Sporobolus cryptandrus*, *Aristida longiseta*, *Schedonnardus paniculatus*, *Cenchrus tribuloides*, as well as *Senecio oblanceolatus* and *Munroa squarrosa*, a few annuals, the more important of which were *Helianthus petiolaris*, *Verbena bracteosa*, and *Cryptanthe ramosissima*. Into this area *Bouteloua oligostachya* was pushing its way and had in places near the edge of the field almost replaced the other species.

Several miles west and south of Fountain, Col., a most interesting stage of succession is shown. The surrounding vegetation is of the *Bouteloua oligostachya* consocies with very few primary and secondary species. An area which had been broken and abandoned showed the *Muhlenbergia gracillima* consocies almost entirely replacing the earlier stages of the succession. A very little *Boebera papposa* and *Schedonnardus paniculatus* remained, while about an equal amount of *Bouteloua oligostachya* was invading and will after a number of years replace the Muhlenbergia.

As long as the ants are alive, they remove all vegetation for some distance around their hills. In low places *Cleome serrulata* may form a semicircular zone on the lower side of this denunded area. *Helianthus annuus*, *H. petiolaris*, *Stipa Vaseyi*, and many other species may also be found in this situation. The most common plant to develop in this area is *Munroa squarrosa*, which often forms a perfect zone.

Erosion.

The dry soil is easily washed away by heavy rains. This forms loose soil at the base of the hills and also leaves broken places from which the soil is removed. On the hillsides there are often produced natural terraces, each of which ends in a broken edge. During the rains these terraces are cut back and new soil is exposed. These places may be occupied by *Boebera papposa*, *Salsola Tragus*, or other annuals, but generally *Stipa Vaseyi* is the invading species. Here it serves to bind the soil and prepare the way for *Muhlenbergia gracillima* and *Bouteloua oligostachya*.

In the low draws there is generally a hollow washed out below the terrace, and as a result of the falling in of the soil when dry there is found both loose and undisturbed soil. These places are marked by a growth of *Stipa Vaseyi*, with *Boebera papposa*, *Solanum rostratum*, and often *Salvia lanceolata*, *Helianthus annuus*, *Verbena bracteosa*, *Salsola Tragus*, *Xanthium commune*, and *Leptilon canadense*. Places such as this are very much like the ordinary draw where more or less of the soil which was washed down from the hills is deposited. Conditions here are also almost the same as in the alluvial fans which are formed at the bases of all the ravines, whether they be small or large. Here new soil is deposited during every heavy rain, and as a result the slow growing grasses such as *Bouteloua oligostachya* and *Muhlenbergia gracillima* cannot thrive. *Stipa Vaseyi* is the most successful plant of such habitats. It marks the dry water courses and also all of the alluvial fans. Succession here is practically the same as on any ruderal area. In addition to *Stipa Vaseyi* there is usually found *Boebera papposa*, *Salvia lanceolata*, and in some cases *Xanthium commune* and *Cleome serrulata*. When the soil has become more stable *Stipa Vaseyi* slowly gives way. *Artemisia frigida* is now one of the first species to appear, and is often dominant after *Stipa Vaseyi* has disappeared entirely. This is followed by *Muhlenbergia gracillima*, and after a number of years this is replaced in turn by *Bouteloua oligostachya*.

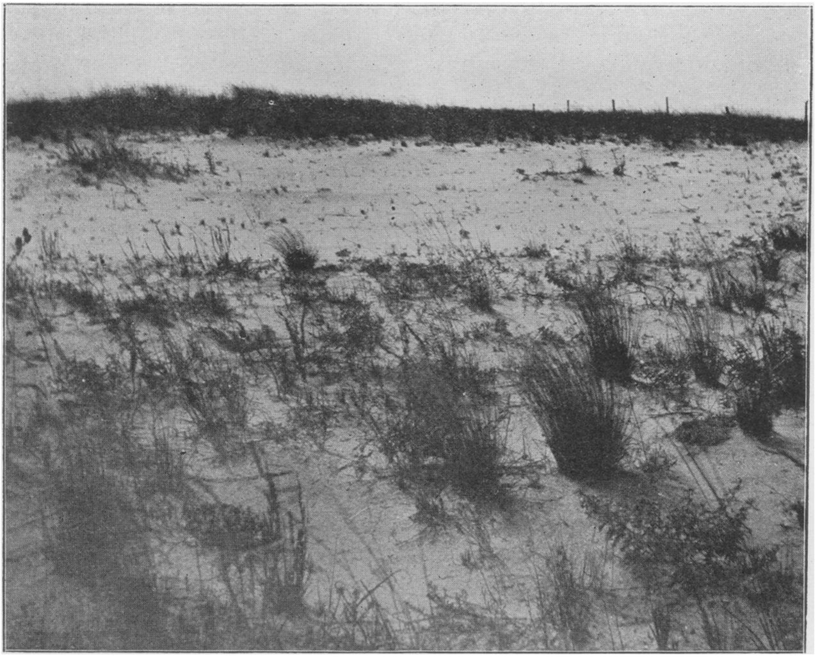

FIG. 13.—Blow-out; the prominent plants are *Muhlenbergia gracilis*, *Meriolix serrulata*, *Artemisia canadensis*, and *Andropogon scoparius*; *Calamovilfa longifolia* in the background.

On dry sandy ridges blow-outs are often found (*fig. 13*). The succession here is usually *Polygonella articulata*, *Cycloloma atriplicifolium*, *Carex* sp., *Muhlenbergia gracilis*, *Sporobolus cryptandrus*, *Artemisia canadensis*, *Thelesperma gracile*, *Eriogonum annuum*, *Meriolix serrulata*. *Chrysopsis villosa*, and *Andropogon scoparius*.

The most important plant occupying the alluvium deposited by permanent streams is *Melilotus alba.* Species of minor importance are *Juncus bufonius* and *Riccia crystallina.*

ANOMALOUS SUCCESSION.

When biotic or physical agencies bring about sufficient change in the habitat, the result is an anomalous succession. The change of habitat may be gradual and yet the effect on the succession be such as will change entirely the ultimate formation. We may also have the succession interfered with in such a way as to hasten the ultimate formation, to cause it to become more stable in a shorter time, or to retard the succession or reduce it to a more primitive condition.

Due to grazing.

The influence of grazing is very clearly seen by comparing fenced areas with those that have not been protected from grazing animals. Cattle, and to a less extent horses, are the only animals that have grazed within this region in recent years.

Near the lower end of the mesa is Colorado City, the old territorial capital of Colorado and known as one of the oldest towns in the state. For fifty years it has been the custom to have a herd boy drive the cattle out on the adjacent areas to graze each day and bring them back each night. Colorado Springs, a more recent city, also sends its herds out on the same area. It will be well, at first, to see what effect this has had upon the Bouteloua formation. In those parts of the formation where grazing has not played a part the formation is very open, while in the grazed portions it is more closed. In the open formations many species appear with the grasses, while in the more closed formation these species are almost entirely absent. A typical quadrat from the south mesa which has been grazed shows the following species:

Muhlenbergia gracillima	23	33%	Sideranthus spinulosus	3
Bouteloua oligostachya	24	12	Malvastrum coccineum	5
Atheropogon curtipendulus	1		Townsendia exscapa	2
Artemisia frigida	2		Echinocereus viridiflorus	1
Boebera papposa	36			

Total surface covered, 45 to 50%.

In some of the draws the preponderance of *Muhlenbergia gracillima* is even more marked. Near the above quadrat, in a portion protected from grazing, a quadrat would show:

Bouteloua oligostachya	18 %	Artemisia frigida	1
Muhlenbergia gracillima	2.5	Artemisia gnaphalodes	1
Aristida longiseta	2.5	Gutierrezia Sarothrae	2
Chrysopsis villosa	8	Sitanion elymoides	1
Thelesperma gracile	9	Eriogonum alatum	2
Echinocereus viridiflorus	4	Pentstemon angustifolius	1
Opuntia polyacantha	3	Carex pennsylvanica	5
Euphorbia robusta	1		

Total surface covered, 27%.

In a portion of the mesa which has been grazed, but not to such an extent as the first quadrat given, is found:

Bouteloua oligostachya	22%	Artemisia frigida	5%
Muhlenbergia gracillima	7		

It cannot be stated positively that this condition is entirely due to grazing. It seems likely, however, that grazing would favor the development of grasses and tend to destroy the other plants, particularly the dicotyledons. There is a very noticeable difference in adjacent areas when one is protected from grazing. The preponderance of *Bouteloua oligostachya* and *Muhlenbergia gracillima*, and the paucity of higher spermatophytes in the grazed area is the chief difference. This seems to be the exact condition which would come about by natural succession and the grazing in this case hastens this succession. The more primitive parts of the formation and those which have not been grazed are much alike. Grazing, when not too severe, favors the development of the facies of the formation.

Still another condition due to grazing should be considered. Near Colorado City, and particularly in the region lying between Colorado City and Colorado Springs, the grazing has been very severe. The result here has been first to drive out most plants other than the grasses, and ultimately even to destroy *Bouteloua oligostachya* and *Muhlenbergia gracillima* to a great extent. A few plants, such as *Astragalus bisulcatus*, *Chrysothamnus graveolens*, *Grindelia squarrosa*, and others which are not touched by grazing animals, still survive; but the character, aside from a few of these species, is now almost entirely marked by annuals. The succession has become practically that which follows on a denuded area. *Salvia linearis*, *Atriplex argentea*, and *Bouteloua prostrata* are here the principal species. With these are found many of the ruderal plants as well as the following important perennials: *Agropyron occidentale*, *Astragalus bisulcatus*, *Sophora sericea*, *Vicia americana*, and a very little *Bouteloua oligostachya*, *Quincula lobata*, and *Phyllopterus montanus*.

The effect is to delay the succession or to cause it to return to a more primitive condition. The grazing does not change the Bouteloua formation into another formation, since grasses seem to be especially adapted to these conditions.

The effect of grazing is very different on the thicket formation. Wherever cattle are allowed to crop the thicket formation very closely, the facies are completely killed. This is the most noticeable in the case of the oaks, which are killed by the entire loss of chlorenchyma tissue. They are attacked by cattle before any of the other facies of the thicket formation.

An examination of the region shows that on the mesa near Colorado City the thicket formation has been replaced almost entirely by the Bouteloua formation. Only scattered bushes of *Cercocarpus parvifolius* and *Rhus trilobata* are found and these much reduced in size. The explanation lies in the fact that this portion has been grazed more than the part which is farther removed from Colorado City. The remnant of the old thicket can be seen in many places, and the stages in the succession which have produced a grass formation instead of a thicket formation may be traced. There is a scanty plant growth under these shrubs. When they are killed outright the space is open to plant invasion, and as a result the ruderals come in in abundance. *Chenopodium album* may be one of the forms which appears at this time, especially if the cattle have destroyed most of the under vegetation. At other places where the shrubs have been cut down the succession may be much the same as the ruderal succession and result in the typical Bouteloua formation. As a rule the shrubs are gradually reduced in size. The result here is that the grasses slowly encroach upon the area as the shrubs are eaten lower, and as the clump becomes more open the undergrowth increases. *Agropyron occidentale*, *Stipa comata*, *S. neo-mexicana*, *Atheropogon curtipendulus* come in slowly; *Coleo-*

santhus umbellatus and *Chenopodium Fremontii* disappear. When the shrub ultimately dies and breaks up, there is a very small ruderal place in which the succession is identical with that already described for denuded places. Grazing changes the thicket formation to a grass formation, and the more rapid the change the more nearly it approaches the ordinary ruderal successions.

Due to drainage.

Drainage is not an important factor, but it seems best to consider here those changes which result when an irrigated area is left without irrigation, a ditch abandoned, or the water of a stream turned aside causing the bed to become dry.

Examples of the first case mentioned are not found excepting where, because of lack of attention, the water does not flow evenly over a meadow. The succession here is gradual, forms like *Erigeron flagellaris*, *Vicia americana*, and *Astragalus hypoglottis* taking the place of the more hydrophytic grasses and rushes. If the change of habitat is abrupt, most of the species die and a ruderal succession follows. When the change is very gradual, the species mentioned above, together with *Agropyron occidentale*, take the place of the rushes. *Bouteloua oligostachya* often appears in this stage of the succession, but *Muhlenbergia gracillima* is one of the last to appear.

In abandoned ditches a mixed formation is generally found. In this habitat the following species of the mesophytic bank formation may continue for a long time: *Clematis ligusticifolia*, *Xanthium commune*, *Symphoricarpos occidentale*, *Stachys palustris*, *Erigeron flagellaris*, and *Vicia americana*. The last two species are elements of the Bouteloua formation and are able to adapt themselves to the change of habitat. Of the grasses of the Bouteloua formation, *Bouteloua oligostachya* and *Agropyron occidentale* are the first to enter. They appear much earlier than *Muhlenbergia gracillima*, and thrive even better in these transformed ditches than in the Bouteloua formation proper.

There is only one example of the effect of a change in the natural water course. This is not complete, but enough water has been taken from Camp Creek to cause it to be dry for a greater part of the year. The first and most noticeable effect has been the death of the trees, *Populus angustifolia* and *P. deltoides*. This condition has obtained for only about three years, and the effect thus far has been destructive. The bank species, with the exception of those that are able to exist in more xerophytic habitat, have died, and aside from the entrance of a very few ruderals there has been no marked succession as yet.

Due to irrigation.

The changes produced by irrigation are complete and varied. Where a ditch passes through the Bouteloua formation in places where there is seepage, the first stages of the succession which lead to the irrigated meadow formation are found. The effect here is usually the better development of *Agropyron occidentale*, and at the same time the disappearance of *Muhlenbergia gracillima*. *Bouteloua oligostachya* also grows more rank than where not irrigated. This succession is exceedingly variable, probably because of the variable water supply, and the stage of the succession is an index to the amount of water added. In some places the meadow flora is reduced largely to rushes and other hydrophytic plants, while in other places *Bouteloua oligostachya*, *Erigeron flagellaris*, *Vicia americana*, and *Astragalus hypoglottis* are most important.

In the bank formation the conditions are varied. Between the water and the xerophytic formation through which the stream or ditch runs, there are all gradations from hydrophytic to xerophytic. But to divide this formation in regard to water content of the soil would not be practicable. Another condition makes the formation more complex. In the ditch formation, there is, besides the invasion of the mesophytic and hydrophytic plants, the entrance of the ruderal. When the ditch is first made the ruderal formation makes its appearance. At almost the same time the mesophytes and hydrophytes appear. The ruderal formation always tends towards self destruction. Here the result is that the outer portion of the ditch is ultimately occupied by the characteristic Bouteloua formation, while on the inner the more mesophytic bank species become established. In the ultimate bank formation the line of separation from the grass formation is very distinct.

Along many of the irrigation ditches a condition prevails which prevents the development of the ultimate stage of the succession. Each year the bottom of the ditch fills up with silt which is removed to the bank the following spring. This forms a new soil for the entrance of ruderal species, and as a result the bank returns to a somewhat primitive condition.

Another factor of importance here is the fact that during the winter the ditch is empty the greater part of the time. This condition is detrimental to the success of the species of the ultimate formation. The result is that along these irrigation ditches are found various stages of anomalous successions, which are checked repeatedly, or even turned back by the reversion to more primitive conditions. The successions are interrupted again and again, and this may account to a great extent for the variable character of the bank formation.

General discussion.

After careful study it is at once apparent that all parts of the formation are not of the same age. The secondary successions throw much light upon the structure as well as upon the development of the formation. These exhibit rather well-marked stages. The first is a ruderal consocies; the second, a society of the formation; while the ultimate stage is a consocies of the formation. All of these successions lead undoubtedly to the Bouteloua formation.

The successive deposition and erosion which has produced the Great Plains does not differ markedly from that which may be noted at the present time. The vegetation on new deposits of soil passes through the typical succession leading from the ruderal to the grass formation. Near the mountains the cutting back of the gullies results in the establishment of the thicket formation, which is preceded usually by the entrance of many of the secondary species of the thicket and grass formation. The pine formation is usually mixed with the thicket formation. When this cutting back of the gullies exposes rocks of a sufficient degree of stability, the primitive lichen formation precedes all others.

In many places gullies are cut back which are reclaimed at once by the grass formation. The thicket and pine formations do not enter. In these places the *Andropogon scoparius* consocies usually becomes established.

The elevated dry ridges are occupied by the *Selaginella densa* formation in which *Paronychia Jamesii* is a prominent species. This evidently represents a younger stage in a succession which will give ultimately the Bouteloua formation. Among the most important invading species are *Stipa comata*, *Koeloeria cristata*, and *Bouteloua hirsuta.*

If these ridges are sandy, blow-outs often occur which result when reclaimed in the *Calamovilfa longifolia* consocies (*fig. 13*). This consocies thrives much better when not grazed. Grazing changes it to the Bouteloua consocies.

The *Andropogon scoparius* evidently represents an earlier stage in the formation than the *Andropogon furcatus* or *Bouteloua oligostachya* consocies. It occurs on the hillsides and also is found as an early stage in the succession on denuded xerophytic areas. The study of secondary succession would lead also to the belief that *Muhlenbergia gracillima* is only a stage, for here it is replaced repeatedly by *Bouteloua oligostachya.*

The societies of the formation are, without exception, dominated by species which are among the first to invade new areas. Their presence in the formation is largely due to historical reasons. To this may be added the fact that the consocies which represent the earlier stages, as for example the *Bouteloua hirsuta* consocies, have by far the greater number of societies.

The *Bouteloua oligostachya* consocies represents the ultimate stage of the grass formation and is by far the most widely distributed of any of the consocies of the formation.

This study of the Bouteloua formation was suggested by Professor FREDERIC E. CLEMENTS, under whose direction it has been carried on. To him and also to Professor CHAS. E. BESSEY the writer wishes to express his thanks for many helpful suggestions and criticisms. Thanks are also due to the following persons: Professor F. D. HEALD, for advice and criticism; Professor WM. STRIEBY, for generously giving me use of his laboratory for the determination of water content; and to Professor F. H. LOUD, for meteorological data.

UNIVERSITY OF MISSOURI, COLUMBIA.